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A review of regulation ecosystem services and disservices from faunal populations and potential impacts of agriculturalisation on their provision, globally

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Abstract

Land use and cover change (LUCC) is the main cause of natural ecosystem degradation and biodiversity loss and can cause a decrease in ecosystem service provision. Animal populations are providers of some key regulation services: pollination, pest and disease control and seed dispersal, the so-called faunal ecosystem services (FES). Here we aim to give an overview on the current and future status of regulation FES in response to change from original habitat to agricultural land globally. FES are much more tightly linked to wildlife populations and biodiversity than are most ecosystem services, whose determinants are largely climatic and related to vegetation structure. Degradation of ecosystems by land use change thus has much more potential to affect FES. In this scoping review, we summarise the main findings showing the importance of animal populations as FES providers and as a source of ecosystem disservices; underlying causes of agriculturalisation impacts on FES and the potential condition of FES under future LUCC in relation to the expected demand for FES globally. Overall, studies support a positive relationship between FES provision and animal species richness and abundance. Agriculturalisation has negative effects on FES providers due to landscape homogenisation, habitat fragmentation and loss, microclimatic changes and development of population imbalance, causing species and population losses of key fauna, reducing services whilst enhancing disservices. Since evidence suggests an increase in FES demand worldwide is required to support increased farming, it is imperative to improve the understanding of agriculturalisation on FES supply and distribution. Spatial conservation prioritisation must factor in faunal ecosystem functions as the most biodiversity-relevant of all ecosystem services and that which most closely links sites of service provision of conservation value with nearby sites of service use to provide ecosystem services of agricultural and economic value.

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Keywords
crop raiding, disease control, providers, invasive species, pest control, pollination, seed dispersal

Introduction

Biodiversity is recognised as a key support for stable life on Earth (Hautier et al. 2015) and plays an essential and complex role in all levels of ecosystem services production (Pimentel et al. 1997, Balvanera et al. 2006, Mace et al. 2012). To properly manage, value and conserve ecosystem services (ES), it is essential to have an accurate definition and characterisation of the services and the traits that underpin them. Ecosystem service providers are the species or entities on which the service provision depends and identifying and characterising their functional relationships are amongst the key research areas to increase understanding of the link between biodiversity and ecosystem services production (Luck et al. 2003, Kremen 2005, Duncan et al. 2015).

Animals are key ecosystem services providers; therefore, we denominate faunal ecosystem services (FES) as those services that rely heavily on animal population. Fauna is a source of provisioning (e.g. Henchion et al. 2014), cultural (e.g. Villamagna et al. 2014) and regulation (e.g. Kremen et al. 2007) services. For the latter, animals perform functions that allow ecosystem maintenance and thus production of other services, such as food or fibre provision. Conserving animal populations that provide FES is essential to maintain the correct functioning of ecosystems to provide ecosystem services where there is demand for them.

An imbalance of animal populations may be the cause of reduced FES production and/or the generation of faunal ecosystem disservices, such as the occurrence of crop pests (e.g. Rasmussen et al. 2017) and the spread of zoonotic diseases to humans (e.g. McCauley et al. 2015). Evidence suggests that such an imbalance can result from land use and cover change (LUCC), the dominant form of which globally is agriculturalisation of natural ecosystems (e.g. Wilby and Thomas 2002, McCauley et al. 2015). LUCC is considered the most important driving force of biodiversity and ecosystem function loss (MA 2005, Bastian 2013).

Regulation FES occur mostly at the local scale (Kremen et al. 2007) and the assessment of their provision and effects of LUCC has been evaluated at this scale (e.g. Kremen et al. 2002, Levey et al. 2008, Chaplin-Kramer et al. 2011). Although many studies have focused on finding spatial congruence between faunal diversity and regulation ecosystem services at large scales (Naidoo et al. 2008, Luck et al. 2009), these studies assess groups unlikely to produce a direct influence on the regulation services, e.g. linking diversity of vertebrates to carbon storage (Strassburg et al. 2010) or threatened species to freshwater provision (Larsen et al. 2011). This research is limited to describing spatial patterns of biodiversity and ecosystem services but does not assess the underlying role of faunal diversity in providing regulation ecosystem services. The direct relationship between animal diversity and regulation FES beyond the local scale and understanding the effects of LUCC on FES provision globally remains to be evaluated.

In this scoping review, we aim to give an overview of the current and future situation of regulation FES in response to agriculturalisation globally. We summarise the most relevant evidence addressing the following topics: a) the relevance of animal populations as providers of regulation services; b) the role of species richness and of abundance of providers in regulation FES provision; c) animal populations as a source of ecosystem disservices, d) the effects of agriculturalisation on FES providers, e) the mechanisms underlying the observed negative impact of provider loss on regulation FES provision, f) the potential condition of regulation FES under future LUCC and g) the expected demand of regulation FES worldwide.

Rationale

First, we summarise the evidence available to support the FES concept, which highlights animal populations as essential providers of animal pollination, biological control (including pest and disease control) and seed dispersal, as fundamental regulation services operating in both natural ecosystems and agriculture. Hereafter, the topics included in the review are addressed per service, in the order given.

ES provision has been used as a strong argument for biodiversity conservation (e.g. Balmford et al. 2002, Balvanera et al. 2006, Cardinale et al. 2011, Bastian 2013) and, simultaneously, this idea has been widely debated (e.g. Schwartz et al. 2000, Balvanera et al. 2001, Kleijn et al. 2015). Ecosystem services are by definition a function of supply and demand (there is no service without demand for it) and for many services proximity to demand is key. Many non-FES services are as much a function of climate, landscape and ecosystem structure as they are of biodiversity or species abundance. We give an overview of the role of richness and abundance in regulation FES provision to assess if FES provision can more directly support faunal conservation than other types of ecosystem service provision.

This is followed by the evidence showing the negative impacts on human well-being that can be produced by animal populations under agriculturalisation, which are referred to as faunal ecosystem disservices (Lyytimäki and Sipilä 2009, Shackleton et al. 2016). Like all the components of ecosystems, animal populations can be a source of benefit or can undermine human well-being (Zhang et al. 2007, von Döhren and Haase 2015; Figure 1). It has been recognised that the occurrence of services and disservices is part of a continuum and must be examined together to improve the understanding of their relationship with biodiversity (Shackleton et al. 2016). We address the faunal disservices caused by both invasive and native species including spread of human diseases, crop pests and crop raiding.

Finally, we synthesise evidence indicating the causes of loss of FES providers in response to the consequences of agriculturalisation: landscape homogenisation, habitat fragmentation and loss, microclimatic changes, proliferation of pests and use of pesticides. We describe the impacts of loss of FES providers on provision. It is worth mentioning that we make a distinction between the effects on providers and on provision because the former indicates the causes of loss and the latter its consequences.

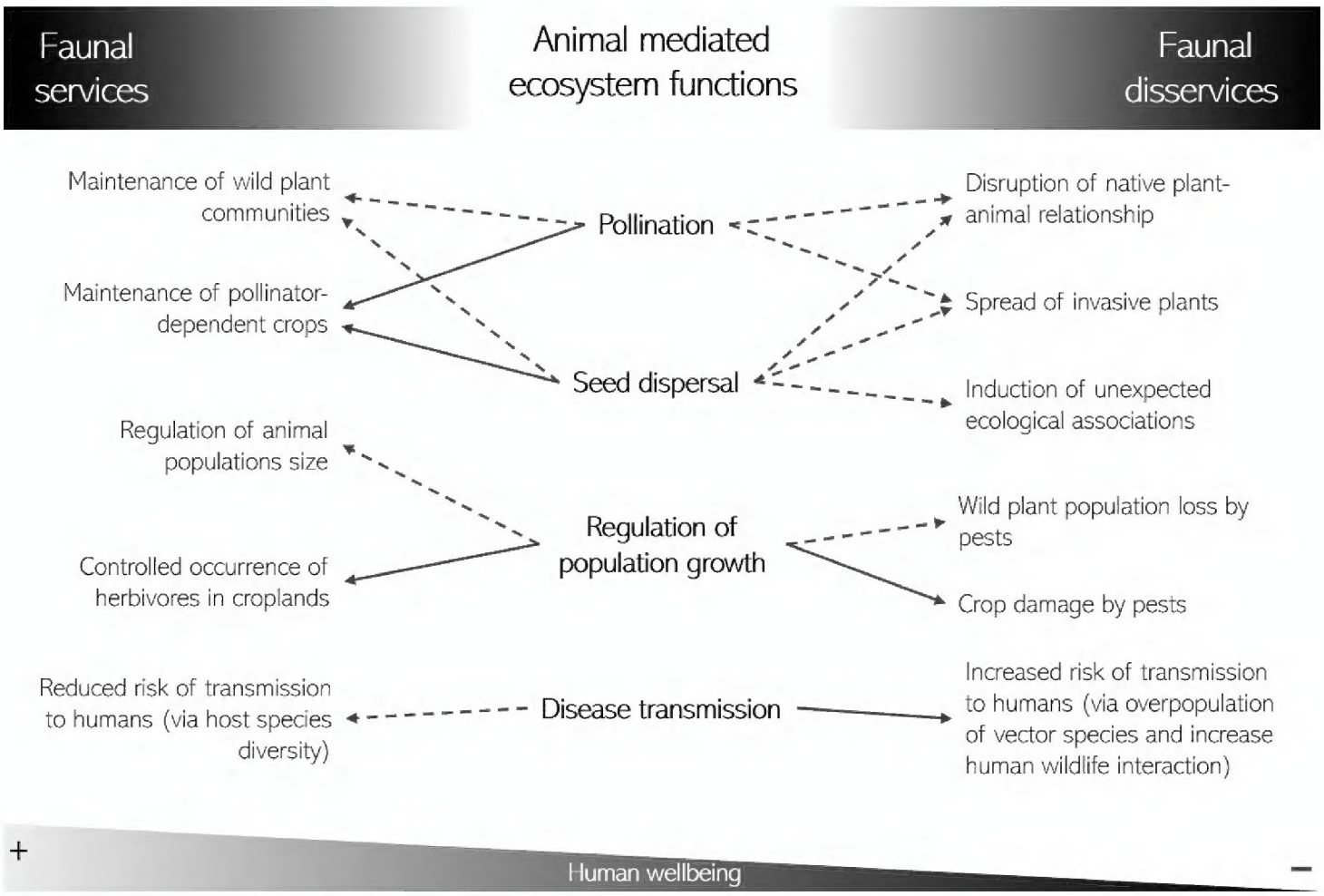
Faunal services
Animal mediated ecosystem functions
Faunal disservices
Maintenance of wild plant communities
Maintenance of pollinator-dependent crops
Pollination
Seed dispersal
Disruption of native plant-animal relationship
Spread of invasive plants
Induction of unexpected ecological associations
Regulation of animal populations size
Controlled occurrence of herbivores in croplands
Regulation of population growth
Wild plant population loss by pests
Crop damage by pests
Reduced risk of transmission to humans (via host species diversity)
Disease transmission
Increased risk of transmission to humans (via overpopulation of vector species and increase human wildlife interaction)
+
Human wellbeing
−

Figure 1. Animal populations as source of services and disservices. The same ecosystem function mediated by animal populations may enhance (faunal service) or undermine (faunal disservice) human wellbeing and it can manifest directly (solid arrows) or indirectly (dashed arrows).

Having addressed the present situation of FES and impacts of agriculturalisation, we address the potential trajectories for FES in the future based on the few studies that have used modelling to project agriculturalisation over the next decades and which have also assessed the impact on regulation services. Finally, we assess the expected demand for FES worldwide, given projected population growth and agricultural expansion since service provision cannot be assessed unless changes in demand are understood.

Regulation faunal ecosystem services

Ecosystem functions can produce ecosystem services (benefits or goods) where there is human demand. A key suite of these services are the regulation services (Haines-Young and Potschin 2011). Animal populations are essential providers of the following regulation services: 1) animal pollination, for which insects, especially bees, are the major providers (e.g. Kremen et al. 2002, Klein et al. 2007); 2) natural pest control, provided mainly by vertebrate predators (e.g. Mols and Visser 2007, Maas et al. 2016) and parasitoid invertebrates (e.g. Letourneau et al. 2015); 3) human disease control provided by vertebrates (e.g. tick-borne diseases, Ostfeld and LoGiudice 2003, McCauley et al. 2015); and 4) seed dispersal, where providers are mostly birds and flying mammals (e.g. McConkey and Drake 2006, García and Martínez 2012).

The assessment of regulation FES provision is complex, since populations of providers form intricate ecological relationships (e.g. Perfecto and Vandermeer 2006). It requires identification of the community structure that influences ecosystem function and assessment of the key factors affecting such provision, along with the spatial and temporal scale at which providers and services operate (Kremen 2005). FES providers can include a single population (e.g. Hougner et al. 2006), multilevel taxonomic groups (e.g. Blanche and Cunningham 2005, Maas et al. 2013) and different functional groups (e.g. Letourneau et al. 2015). Since service provision assumes a demand for the service, we must also understand the drivers and spatial distribution of that demand.

Most studies in which animal pollination and biological control are evaluated have been carried out in agroecosystems (Table 1), due to the relevance of these FES on crop yield, food supply and the role of providers in agricultural economy (Ricketts et al. 2004, Blanche and Cunningham 2005, Morandin and Winston 2006), while seed dispersal has been evaluated mostly in natural ecosystems, where it is fundamental to understand plant community composition (Wenny et al. 2016). These studies have been carried out throughout the world, mostly at the local scale.

There is a wide range of measures used to assess FES provider contributions to different services (Table 1) and methods vary from purely observational (i.e. natural conditions, e.g. McConkey and Drake 2006) or experimental (i.e. controlled conditions, e.g. Maas et al. 2013, Garratt et al. 2016) to a combination of both (e.g. Hougner et al. 2006, Egerer et al. 2018). Below, we summarise the evidence per service, showing the relevance of animals as FES providers.

Animal pollination

Animal pollination is a fundamental process in terrestrial ecosystems and is essential for maintenance of wild plant communities and agricultural systems (Potts et al. 2010). Faunal pollination is a key ecosystem service in agricultural productivity. In contrast with the other regulation FES, the contribution of animal pollination has been widely quantified.

According to Klein et al. (2007), 35% of crops depend on pollinators globally, while Kremen et al. (2002) estimated 66% for the 1,500 crop species of the world amounting to between 15 and 30% of food production. Williams (1996) estimated for European crops that over 80% of the 264 species assessed require animal pollination. Roubik (1995) estimated that productivity of approximately 70% of tropical crops is improved by animal pollinators. Regarding wild plant species, 80% of flowering plants are directly dependent on insect pollination for fruit and seed set globally (Klein et al. 2007, Ollerton et al. 2011).

Given the morphological diversity of plants, the degree of self-compatibility and the diversity of reproductive organs in the flowers of crops, a great diversity of vectors is required for efficient animal pollination (Williams 2002, Blüthgen and Klein 2011). Insects are the most important animal pollinators by virtue of their abundance and foraging behaviour (Williams 2002). Thousands of species of bees, flies, wasps, beetles,

Table 1. Faunal ecosystem services. Selected examples of studies where regulation ecosystem services provided by fauna are assessed, describing the providers, ecosystem benefited by the service and service quantification measure.

Ecosystem service	Service provider	Ecosystem	Measure	Study site	Reference
Pollination	Native bees	Agroecosystem (watermelon crops)	Pollen deposition	Yolo County, California, USA	Kremen et al. (2002)
	Exotic and native bees	Agroecosystem (coffee plantation)	Seed mass, fruit set, peaberry frequency, pollen deposition, bee species richness	Finca Santa Fe, Valle General, Costa Rica	Ricketts et al. (2004)
	Nitidulid and Staphylinid beetles	Agroecosystem (atemoya crops)	Beetle species richness	Atherton Tableland, Queensland, Australia	Blanche and Cunningham (2005)
	Wild bees	Agroecosystem (canola crops)	Bee abundance, seed set	La Crete, Alberta, Canada	Morandin and Winston (2006)
	Ceratopogonids midges	Agroecosystem (cocoa and plantain crops)	Midges abundance, pod set, intercropping proportion	Kubease, Abrafo-Ebekawopa and Edwenease, Ghana	Frimpong et al. (2011)
	Hoverfly, solitary mason bee and bumblebee	Agroecosystem (apple orchards)	Flower visitation, fruit set	Reading and Leeds experimental farms, UK	Garratt et al. (2016)
Pest control	Parasitoid eggs (Mirid bug, Wolf spider, Tetragnathid spiders)	Agroecosystem (rice crops)	Plant- and leaf-hoppers abundance	Luzon, Ifugao, Philippines	Drechsler and Settele (2001)
	Aztec ant and Green scale (mutualism avoids occurrence of coffee berry borer)	Agroecosystem (coffee plantation)	Ant activity, green scales abundance	Finca Irlanda, Chiapas, Mexico	Perfecto and Vandermeer (2006)
	Great Tits	Agroecosystem (apple orchards)	Percentage of caterpillar damage per apple tree	Netherlands	Mols and Visser (2007)
	Birds and bats	Agroecosystem (cacao plantations)	Herbivorous insect abundance, final crop yield	Napu Valley, Central Sulawesi, Indonesia	Maas et al. (2013)
	Birds and bats	Agroecosystem (coffee plantation)	Herbivorous arthropod abundance and leaf damage proportion	Finca San Antonio and Hacienda Rio Negro, Coto Brus Valley, Costa Rica	Karp and Daily (2014)
	Parasitoid wasps and flies	Agroecosystem (cruciferous crops)	Parasitoid richness, abundance of parasitised cabbage by aphids and loopers	Monterey, Santa Cruz, and San Benito Counties, California, USA	Letourneau et al. (2015)
	Leaf beetles, root and flower-feeding weevils	Wetland	Purple loosestrife cover, occurrence of feeding damage and abundance of biological control agents	Minnesota, USA	Wilson et al. (2004)
Human diseases control	Mammals, birds and reptiles	Temperate forest	Infected ticks with Lyme disease proportion	Southern New York State, USA	Ostfeld and LoGiudice (2003)
	Birds	Forested urban to rural areas	Bird diversity, mosquitoes and humans infected West Nile virus	St Tammany Parish, Louisiana, USA Ozark forest, Missouri, USA	Ezenwa et al. (2006)Allan et al. (2009)

Ecosystem service	Service provider	Ecosystem	Measure	Study site	Reference
Human diseases control	Small wild mammals	Desert (Caatinga) Tropical forest (Amazon) Wetland (Pantanal)	Small mammal diversity and abundance, dogs infected with Chagas disease	Amazon Basin, Brasil	Xavier et al. (2012)
	Rodents	Evergreen forest and Agroecosystem (mainly maize crops)	Infected rodents with bubonic plague abundance	Tloma village, Kambi ya Nyoka village and Manyara region, Tanzania	McCauley et al. (2015)
Seed dispersal	Eurasian jay	Oak forest (National Urban Park)	Oak saplings abundance	National Urban Park of Stockholm, Sweden	Hougner et al. (2006)
	Flying fox	Tropical forest	Flying fox abundance, chewed diaspores	Vava'u Islands, Tonga	McConkey and Drake (2006)
	Thrushes	Temperate secondary forest	Seed abundance and richness and frugivorous abundance and richness	Cantabrian Range, Spain	García and Martínez (2012)
	Native frugivore birds	Tropical forest (Wild chillies)	Seedling emergence of gut passed seeds vs. non-gut passed seeds	Guam, Mariana Islands	Egerer et al. (2018)

butterflies and moths contribute to pollination of many crops, such as gourds, oilseeds, berries and tobacco, amongst many others (Roubik 1995, Williams 2002, Blanche and Cunningham 2005), as well as a countless number of wild plant species. Bees are probably the most recognised pollinators (>12,000 species; e.g. Kremen et al. 2002, Larsen et al. 2005, Morandin and Winston 2005, Potts et al. 2010, Kerr et al. 2015).

Biological control of pests and human diseases

Biological control is the natural process responsible for the regulation of species' population growth through ecological interactions –mutualism, parasitism and predation. This has been highlighted as a relevant regulation FES given the key role in restraining the spread of crop pests and diseases (Wilby and Thomas 2002, Fiedler et al. 2008, Karp and Daily 2014).

Oerke (2006) made an estimation of potential and actual losses due to pests for wheat, rice, maize, potatoes, soybeans and cotton, between 2001 and 2003, worldwide. Arthropod pests destroy 8–15% of these crops and without natural biological control and pesticides, this figure could reach 9–37%. According to the estimation done by Losey and Vaughan (2006), crop damage due to the absence of arthropod native predators might cost approximately US $4.5 billion more than the actual cost given pest control services.

Predation is one of the best-known mechanisms of biological control for agricultural pests and birds and bats have been identified as the main contributors, by their

predation of species responsible for crop damage (Mols and Visser 2007, Maas et al. 2013, Karp and Daily 2014, Railsback and Johnson 2014). Increasing knowledge of the relevance of predators for pest control has increased the concern to conserve the conditions required to maintain these predators (e.g. Williams-Guillén and Perfecto 2010, Railsback and Johnson 2014).

Parasitoidism is considered another important mechanism of agricultural pest control (Drechsler and Settele 2001, Letourneau et al. 2015). The main providers identified are flies and parasitoid wasps, which lay eggs on or in the body of a host, in this case pest insects, eventually killing the hosts and diminishing the spreading of the pest.

Mutualism has been identified as another mechanism that can contribute to pest control. Perfecto and Vandermeer (2006) provided evidence that the mutualistic relationship between the Aztec ant and a coccid has a positive effect on coffee plants by reducing the numbers of the coffee borer beetle, coffee's main pest. This exemplifies the complexity of biological control mechanisms and how an imbalance in ecological condition can negatively impact this FES.

Disease control is also recognised as a relevant FES (Ostfeld and LoGiudice 2003, Foley et al. 2005, McCauley et al. 2015). Wild and domestic animals are vectors for a wide range of infectious diseases that are potentially transmitted to humans (see Molyneux et al. 2008, Civitello et al. 2015). Healthy populations of animals (i.e. populations with the minimum number of sexually mature individuals required to secure their viability) and high diversity provide less risk of human infection, since the probabilities of vectors (e.g. flies and ticks) targeting humans as hosts decreases with higher availability of other host species (Keesing et al. 2006, Civitello et al. 2015). Disease control is a FES directly related to human health and well-being.

Seed dispersal

Animals are also relevant actors in seed dispersal. They drive plant gene flow, population dynamics and spatial structure in undisturbed habitats and contribute to regeneration of deforested habitats, by moving seeds from one site to another (Russo et al. 2006, García and Martínez 2012). Animals are considered long-distance vectors; they contribute to seed dispersal mainly by defecation and epizoochory (seeds adhere to the outside of animal bodies). These include ants, frugivorous terrestrial, arboreal and flying mammals and frugivorous and/or caching birds (Greene and Calogeropoulos 2002). Animal seed dispersal is an essential mechanism in the maintenance of temperate and tropical ecosystems (García and Martínez 2012) and are particularly important for large-seeded plants (Greene and Calogeropoulos 2002, McConkey and Drake 2006, Wenny et al. 2016). Approximately one-half of seed plant species are dispersed by animals (Wenny et al. 2016, Egerer et al. 2018).

The ecological value of faunal dispersal is well known (Russo et al. 2006, Wenny et al. 2016). However, in comparison with animal pollination and pest control, the quantitative assessment of the seed dispersal service by fauna is scarce. Seed dispersal

benefits are spatially and temporally distant from the mother plant, making them difficult to measure, especially for tree species and species not used directly by humans (Wenny et al. 2016) and further quantitative assessment is required for this FES.

The economic value of animals for seed dispersal is even less well known than their ecological value (Wenny et al. 2016). Some studies have indirectly estimated the value of animal seed dispersal through the economic valuation of associated food and fibre consumed by humans (e.g. Fujita and Tuttle 1991, Paoli et al. 2001). However, studies on direct valuation are scarce. A direct economic valuation is made by Hougner et al. (2006), who value seed dispersal carried out by the Eurasian Jay in an oak forest, through the estimation of the cost of replacing birds by human force.

Some of the studies where the role of animals in seed dispersal has been assessed are in tropical ecosystems. McConkey and Drake (2006) highlighted the relevance of flying foxes to sustain Pacific island forests, since these are the only existing animals capable of dispersing large seeds over long distances in such isolated habitats. Egerer et al. (2018) showed that bird dispersal provides a benefit to wild chilli plants in Guam through increased seedling emergence of gut-passed seeds in comparison to depulped seeds and whole fruits.

The role of richness and abundance of regulation faunal ecosystem service providers

Species richness (i.e. the number species present in a certain area) is considered the most simple and direct measure of biodiversity (Gotelli and Colwell 2001) and has been considered an important trait to evaluate the ecosystem services-biodiversity relationship (e.g. Egoh et al. 2009, Schneiders et al. 2012). There is the assumption that high species richness has a strong positive relationship with ES production and by conserving biodiversity, ES can be secured and improved (de Groot et al. 2010, Cardinale et al. 2011, Cimon-Morin et al. 2013, Isbell et al. 2015). However, this idea has been widely debated (Schwartz et al. 2000, Ridder 2008, Kleijn et al. 2015).

An empirical literature review by Schwartz et al. (2000) found little support for the hypothesis that there is a strong dependence of ecosystem function on species richness. They describe a curvilinear response where ecosystem function reaches saturation at low levels of species richness, indicating that few species can be enough to fulfil ecosystem functions. Equally, Ridder (2008) pointed out that most ES are not provided by all the extant species in a given ecosystem, but by any group of species that meet certain basic functional criteria or by species that are dominant and especially resilient in the face of change. In this sense, they highlight that using this argument could be counterproductive for both biodiversity and multiple ES conservation, since it would focus only on the conservation of a few "functional" species.

In contrast, Hector and Bagchi (2007) concluded that large numbers of species are necessary to fulfil the inherent multi-functionality of ecosystems. As more ecosystem functions were included in their analysis, more species were found to affect the overall

functioning. Isbell et al. (2011) argued that species may appear functionally redundant when only one function is considered under one set of environmental conditions, but many species are needed to maintain multiple functions at multiple times and places. Bastian (2013) argued that species are embedded in an ecosystem and the loss of a single species (or population) and/or ecosystem function might have unpredictable effects. Therefore, conservation of all ES does imply conservation of biodiversity, even though many services are unrelated to species diversity or abundance and more related to climatic and structural properties of vegetation and landscape as well as human demand for them (Mulligan 2018).

Regarding regulation FES, there is evidence that, by increasing species richness, FES provision is improved. For instance, Larsen et al. (2005) showed how a decrease in bee species diversity considerably disrupts the pollination service. The meta-analysis carried out by Civitello et al. (2015), provided evidence that host diversity inhibits wildlife and human parasite abundance. Concerning seed dispersal, García and Martínez (2012) described a positive relationship between frugivorous birds richness and all the indicators of dispersion evaluated.

Abundance (i.e. number of individuals per species), rather than species richness, has been suggested as the most important trait that influence FES occurrence (Harrison et al. 2014, Winfree et al. 2015), particularly for pest regulation and pollination. According to the analysis carried out by Winfree et al. (2015), abundance of the dominant species is the main driver of ES delivery, while rare species are important for species richness but have little contribution to ecosystem functioning.

Some studies have evidenced the relevance of abundance of beetles (Blanche and Cunningham 2005), midges (Frimpong et al. 2011) and bees (Morandin and Winston 2005,2006) for crop pollination. Equally, predator abundance appears to be a determinant for the pest control service (Koh 2008, Crowder et al. 2010, Maas et al. 2013). The evidence above suggests that, unlike for many other classes of ecosystem service, animal species richness and abundance is required to secure regulation FES provision.

Faunal ecosystem disservices

Ecosystem disservices were recently defined as the ecosystem generated functions, processes and attributes that result in perceived or actual negative impacts on human well-being (Shackleton et al. 2016). Although there is literature addressing ecosystem disservices across several scientific disciplines, such as natural disaster management, agriculture and public health (Lyytimäki and Sipilä 2009, von Döhren and Haase 2015, Shackleton et al. 2016), the concept and theoretical framework around it are relatively new and undeveloped compared to that of ecosystem services (Shackleton et al. 2016) and associated literature is scarce (von Döhren and Haase 2015).

For many years, the assessment of the links between ecosystems and human well-being has been focused only on ecosystem services (Lyytimäki and Sipilä 2009). How-

ever, there are strong links between services and disservices: the same ecosystem function or component can be a source of service or disservice simultaneously (Zhang et al. 2007, Limburg et al. 2010, Escobedo et al. 2011; Figure 1).

The designation as service or disservice depends on the perceived influence on human well-being (Lyytimäki and Sipilä 2009). For example, a pollinator insect population can act as service provider by pollinating native plants and act as disservice provider by pollinating invasive plants in the same ecosystem. Therefore, to enhance our understanding of the ecosystem-human well-being relationship, we should aim for an integrative examination of ecosystem services and disservices (Ninan and Inoue 2013, Shackleton et al. 2016).

An integrative and balanced approach to services and disservices provides a better foundation for environmental management and conservation efforts (Lyytimäki 2015). With this aim in mind, Shackleton et al. (2016) proposed a working definition, characterisation and first categorisation for ecosystem disservices. They recognise that manifestation of disservices can be direct, i.e. impacting directly on human well-being (e.g. crop raiding by medium or large sized mammals) or indirect, by diminishing the flow or causing the loss or impairment of ecosystem services (e.g. invasive species altering native pollinator-plant relationships). Regarding categorisation, they consider two main aspects: origin of the disservice as biotic or abiotic and nature of the impact, as economic, health (health and safety) and cultural (aesthetic and cultural). According to this typology, the disservices related to agriculturalisation here termed faunal ecosystem disservices, belong to Shackleton et al's (2016) bio-economic and bio-health categories (Table 2). The disservices addressed here are: impacts of invasive species, spread of human diseases, crop pests and crop raiding.

Invasive species

Effects of invasive species on native species are well documented (e.g. D'Antonio et al. 2004, Alpert 2006) and, more recently, their effects on ecosystem services has also drawn attention (Pejchar and Mooney 2009, Pyšek and Richardson 2010, Peh et al. 2015, Walsh et al. 2016). According to Pejchar and Mooney (2009), the impact of alien species is usually well quantified for provisioning services (food, fibre and fuel). However, impacts on regulation FES are rarely calculated, but are likely to be substantial.

Amongst the reported effects of invasive species on animal pollination services are: the disruption of mutualism between native bees and plants by invasive bees, the range expansion in pollinator-limited invasive plants and consequent distraction of pollinators from native plant species (Stokes et al. 2006, Traveset and Richardson 2006). According to the review made by Morales et al. (2017), the impacts of invasive pollinators on pollination are predominantly negative for native plants, mixed for crops and positive for invasive plants. Although invasive pollinators can be beneficial for some native plants in highly disturbed habitats and some crops in intensively modified agroecosystems (e.g. Ricketts et al. 2004), they cannot replace the role of a diverse pollinator assemblage for wild plant reproduction and crop yield.

Table 2. Faunal ecosystem disservices. Selected examples of disservices related to agriculturalisation caused by fauna, describing providers, type of manifestation: direct or indirect (when causes decrease or loss of a service), category (according to Shackleton et al. 2016) and impact on human well-being.

Provider	Manifestation	Category	Disservice	Reference
Invasive pollinators	Indirect (pollination)	Bio-economic	Disruption of native pollinator-plant relationship, spreading of invasive plants	Traveset and Richardson (2006), Morales et al. (2017)
Herbivore insects	Direct (herbivory)	Bio-economic	Damage to crops	Pimentel et al. (2005)
Birds and mammals	Direct (crop riding)	Bio-economic	Damage to crops	Naughton-Treves and Treves (2005), Ango et al. (2016)
Invasive hosts	Indirect (disease control)	Bio-health	Novel hosts increase incidence of diseases, decrease of vertebrate population increases the risk of transmission to humans	Pejchar and Mooney (2009), McCauley et al. (2015)
Invasive frugivores and herbivores	Indirect (seed dispersal)	Bio-economic	Disruption of native seed disperser-plant relationship, spreading of invasive plants, emergence of new ecological associations	Richardson et al. (2000), Gosper et al. (2005)

Invasive species like weeds, insects and plant pathogens (mainly fungi) can become pests and have major impacts on crops. For instance, a well-documented case is the Mediterranean fruit fly, native from West Africa, but now found worldwide, which causes damage to over 250 types of crops. The cost estimated for California reaches US $1 billion (Mooney 2005). Similarly, Pimentel et al. (2005) made a detailed review of the environmental and economic costs associated with alien species in the United States. Related to crops, pasture and forest losses, they identify 500 weed species, feral pigs, European starlings, over 900 insect species and 20 plant pathogen species, as the main agents. The cost of losses, damages and control techniques reaches an annual value of approximately US $50,000 million.

Animal seed dispersal can be a disservice when this involves the spread of invasive plants. Just like the service, the knowledge on how animals contribute to the success of invasive plants is limited (Gosper et al. 2005). However, several mechanisms have been identified: the invasive plant species rely on common native disperser species with generalist diets; the invasive plant is reunited with the disperser species of its native range — like the case of *Rubus* spp. and blackbirds (*Turdus merula*) in Australia; and a new association between plant and animal can occur — like the case of the accidental spread of seeds of wind dispersed pines, *Pinus* spp., by seed predating cockatoos, *Calyptorhynchus* spp., in Australia (Richardson et al. 2000). Additionally, the dispersal of native plants is affected by the competition of dispersal service from invasive plant species (Gosper et al. 2005).

Equally relevant is the effect of invasive species on disease control: invasive plants and animals can act as novel hosts for diseases. Pyšek and Richardson (2010) provided detailed examples of how several invasive species affect human health, acting as vectors (e.g. rodents and bats as vectors of rabies, leptospirosis and hepatitis) or acting directly (e.g. snake bites).

Spread of human diseases

Overpopulation of disease organisms or disease vector organisms and/or the absence of defence organisms can increase the risk of spread for human disease. Many cases of disease outbreaks in human history have been related with invasive pathogens, due to the continual expansion and interchange of human population worldwide (Dobson and Carper 1996, Pejchar and Mooney 2009). For instance, the introduction of smallpox, measles and typhus with European arrivals to the New World increased mortality of the native human population at unprecedented rates (Dobson and Carper 1996). More recently, the increase of mosquito-borne diseases, like yellow fever and dengue, has been attributed to invasive mosquitoes in America and Asia (Pejchar and Mooney 2009). The negative effect can also be indirect, for example, the invasion of the American plant *Lantana camara* in East Africa. *L. camara* is now the habitat of the tsetse fly, vector of sleeping sickness.

Native species may also represent a risk for human health if the natural control of population growth is altered or if human contact with vectors increases. For instance, Ostfeld and LoGiudice (2003) evidenced how the risk of human exposure to Lyme disease increases due to the decrease in diversity of other hosts for ticks (Lyme disease vectors). Equally, McCauley et al. (2015) showed how changes in rodent and flea community composition due to LUCC, increase the abundance of *Mastomys natalensis*, transmitter of plague, in agricultural habitats in Tanzania.

Crop pests

Since the beginning of agriculture, humans have faced crop pests (Oerke 2006), which have had major impacts in human history. Pests, such as rusts on wheat, ergot on rye potato blight, gypsy moth and the boll weevil, have had deep social and economic consequences (Horsfall 1983). Currently 10–16% of global crop production is lost due to pests (Bebber et al. 2013).

Amongst the known causes of occurrence of crop pests is the imbalance of natural biological control, produced by a change in the abundance of natural enemy populations. For instance, a decrease in predator populations allows the increase of prey population (e.g. Drechsler and Settele 2001, Wilby and Thomas 2002, Karp and Daily 2014). Other causes are the absence of indigenous populations which facilitates the success of invasive species with similar ecological requirements (Pejchar and Mooney 2009) and the concentration of food resources, especially in perennial monocultures (Risch 1981, Altieri 2018). Although crop pests have been present since the appearance of agriculture, modern agricultural practices, like agricultural intensification (e.g. Wilby and Thomas 2002), manipulation of soil fertility and irrigation (e.g. Fuller et al. 2012) and use of chemical pesticides (Rosenzweig et al. 2001) have exacerbated these causes (Tilman 1999).

Crop raiding

Crop raiding is the term used to describe the action of wild animals foraging or trampling crops (Hill 2016). In this context, wildlife is considered a pest. However, this is not produced by an imbalance in wildlife populations, but by the increasing overlap of human and wildlife niches, due to continuous human population growth and the anthropogenic transformation of habitat (Hill 1997, Campbell et al. 2000). The most commonly identified actors are medium and large sized mammals (e.g. monkeys, wild pigs, hippopotamus, elephants; Naughton-Treves 1998, Engeman et al. 2010, Ango et al. 2016), but some studies also refer to small mammals and birds (e.g. Naughton-Treves and Treves 2005). Amongst the identified factors influencing crop raiding are the distance from cropland to natural habitat patches, the crop type and hunting practices (Naughton-Treves 1998). Drought, leading to paucity of production in (non-irrigated) natural lands, can also act as a push factor alongside the pull factor of higher productivity in irrigated or improved agricultural areas (Mulligan 2018).

Literature on this subject is extensive and mostly consists of case studies. The approaches to quantify losses vary considerably and are not comparable from site to site (McGuinness and Taylor 2014). The impacts have been assessed in human settlements adjacent to natural protected areas, where the raiding occurs frequently (e.g. Sekhar 2002, Linkie et al. 2007, Hedges and Gunaryadi 2010). However, there are also studies that address this phenomenon outside of protected areas (e.g. Ango et al. 2016, Chaves and Bicca-Marques 2017).

The extent of damage varies widely depending on where the raiding occurs and the type of crops and wildlife species involved. For instance, the socioeconomic impact might be higher in developing countries in non-protected areas with farmers losing their livelihood and rarely being compensated for the losses, thereby creating antagonism towards wildlife (Linkie et al. 2007). In contrast, in protected areas, prevention and compensation measures are more frequently enforced (Sekhar 2002, Davies et al. 2011).

The approaches to estimate monetary losses are variable, varying in unit of measurement and spatial scale. For example, Chakravarthy and Thyagaraj (2005) estimated a loss of US $8 per kilogram of dry capsules of cardamom caused by the Bonnet macaque (*Macaca radiate*), while Engeman et al. (2010) estimated that Rhesus macaque (*Macaca mulatta*) and Patas monkey (*Erythrocebus patas*), both invasive species, causes a nationwide economic impact of US $1.46 million per year in Puerto Rico.

Human-driven environmental changes strongly influence the occurrence of faunal disservices. Simultaneously, these environmental changes have an adverse effect on faunal services through the negative impact on the providers, mainly caused by the loss or transformation of habitat.

Effect of agriculturalisation on regulation faunal ecosystem service providers

Agriculturalisation is considered to be the main driver of loss, modification and fragmentation of habitats, causing biodiversity loss and ES degradation globally (Gaston et

al. 2003, MA 2005). Ramankutty and Foley (1999) estimated that nearly 10.7 million km^2 of forests/woodlands and savannahs/grasslands have been transformed to agricultural land globally between 1700 and 1990. Temperate regions of developed countries experienced the greatest changes during nineteenth century, whilst most tropical developing countries have faced the greatest change from the late twentieth century to the present (Goldewijk 2001). In the past, the change conversion was mostly natural grasslands, whilst currently forests are the agricultural frontier. During the period from 1990 to 2015, there was a net loss of 129 million ha of forests worldwide (FAO 2015). Tropical forests present the highest rates of LUCC (anual rate 0.13%; FAO 2015), mainly for industrial export agriculture, traditional shifting agriculture and cattle ranching (Grau and Aide 2008).

Landscape homogenisation and habitat fragmentation

Landscape heterogeneity refers to the variety of different landscape conditions within a landscape (i.e. area that is spatially heterogeneous in at least one factor of interest, Turner and Gardner 2015) as with mixed habitats or land cover types. A closely related concept is landscape complexity, which can be defined as the level of difficulty observed in understanding the interactions of the landscape components (Papadimitriou 2010). The relationship between these concepts is controversial. Heterogeneity has been described as a function of complexity (e.g. Chen and Xu 2015), at the same time, heterogeneity has been considered an attribute of complexity (e.g. Papadimitriou 2010); furthermore, the terms have been used interchangeably (e.g. Miles et al. 2012).

The inconsistency in the use of terms makes the comparison and synthesis of studies difficult (Reyes Sandoval 2017). However, for practical purposes, we consider that loss of complexity/heterogeneity or landscape homogenisation/simplification refers to the same phenomenon: loss of components and/or loss of the interaction amongst components in a landscape.

The idea that the diversity of landscape components is a key determinant for biodiversity is widely accepted (Fahrig et al. 2011, Katayama et al. 2014). Increased landscape heterogeneity is generally associated with increased biodiversity, since high habitat and resource diversity allows high diversity of species, while the opposite, i.e. landscape homogeneity, is associated with low biodiversity (Parks and Mulligan 2010, Stein et al. 2014).

A consequence of LUCC due to agriculture is landscape homogeneity, as different land cover and habitat types are converted to more uniform agricultural land. Therefore, the proportion of agricultural land is the most commonly used indicator of homogenisation in studies where the relationship between biodiversity and landscape heterogeneity is assessed (e.g. Letourneau et al. 2015, Maas et al. 2016, Jonason et al. 2017). Other indicators include distance from original habitat (e.g. Blanche and Cunningham 2005, Ricketts et al. 2008) and diversity and management indices (Gardiner et al. 2009, Williams-Guillén and Perfecto 2010, Chaplin-Kramer et al. 2011).

Several studies support a positive relationship amongst landscape heterogeneity, species diversity and abundance of FES providers (Table 3). Although neutral or mixed relationships have also been evidenced (Jonsen and Fahrig 1997, Chaplin-Kramer et al. 2011), due mostly to species' particular ecological traits and range sizes (Katayama et al. 2014), landscape heterogeneity has proven to be a relevant factor in ecosystem functioning and population dynamics. Sustainable landscape management is suggested as the most important means of maintaining healthy populations of FES providers (Ricketts et al. 2008, Maas et al. 2013, Letourneau et al. 2015). There is also evidence that homogenised landscapes favour the occurrence of disservices by reducing the diversity and abundance of beneficial arthropods, such as pollinators and parsitoid insects and vertebrate predators (e.g. Letourneau et al. 2015, Senapathi et al. 2015, Maas et al. 2016) and thus increasing the outbreaks of herbivore and diseases pests (e.g. Altieri 1999, McCauley et al. 2015).

Along with landscape homogenisation, agricultural intensification has led to original habitat loss and concurrently to habitat fragmentation. Habitat fragmentation refers to the reduction of continuous tracts of habitat to smaller, spatially distinct remnant patches (Wilson et al. 2016). Fragmentation alters habitat connectivity and quality, affecting biodiversity and ecosystem functioning negatively (Haddad et al. 2015). Equally, reduction of the original habitat of animal populations has increased the conflict between humans and wildlife and the risk of disease transmission (Campbell et al. 2000, Xavier et al. 2012).

The degradation of ecosystems by landscape homogenisation, habitat loss and fragmentation results in decreased carrying capacity to sustain all the organisms that inhabit these ecosystems, leading to continued population losses. The loss of populations precedes species extinction and, therefore, the reduction of biodiversity (Ceballos and Ehrlich 2002).

Several studies have suggested that the loss of genetically distinct populations globally is both absolutely and proportionally several times greater than the rate of extinction of species (Hughes et al. 1997, Ceballos and Ehrlich 2002, Gaston et al. 2003). Genetic variation amongst and within populations confers resilience to environmental change whereas the loss of individuals or populations increases the vulnerability of species, destabilises ecosystem functions and affects ES provision (Luck et al. 2003).

Population losses through habitat loss

Habitat loss and fragmentation are the main causes of population decline (Fahrig 1997, He and Hubbell 2011, Wilson et al. 2016). Hughes et al. (1997) estimate the population diversity, defined as the number of populations on the planet, for 82 species (35 vertebrates, 23 plants, 19 arthropods, four molluscs and one platyhelminth) in the range 1.1–6.6 billion populations. By using the midrange estimation (3 billion populations), assuming a linear function between population and habitat loss and that two-thirds of all populations exist in tropical regions, they estimate that 16 million populations are lost annually across these 82 species alone.

Table 3. Faunal ecosystem service providers and landscape heterogeneity. Examples of studies evaluating the relationship of landscape heterogeneity and FES providers richness and abundance, including the definition of heterogeneity as described by the studies' authors.

Group	Study type	Description of landscape heterogeneity	Relationship	Reference
Native bees	Original	Watermelon farms with gradient of agricultural intensification, 1% to ≥30% natural habitat within a 1-km radius	Positive	Kremen et al. 2002
Nitidulid and Staphylinid beetles	Original	Atemoya orchards with gradient of decreasing distance (0.1–24 km) from tropical rain forest	Positive	Blanche and Cunningham 2005
Bees, bumblebees and beetles	Meta-analysis	Isolation of several crops from natural habitats	Positive	Ricketts et al. 2008
Coccinellid beetles	Original	Soybean and corn crops with gradient of agriculturally dominated to forest and grassland dominated within a 3.5-km radius, landscape diversity measured as Simpson's D	Positive	Gardiner et al. 2009
Pollen beetles, stem weevils	Original	Various crops with gradient ranging from structurally poor to complex landscape at several spatial scales (250–2000 m radius), landscape diversity measured with Shannon-Wiener index	Mixed (Scale-dependent)	Zaller et al. 2008
Leaf-Nosed Bats	Original	Coffee plantations and forest fragments along a gradient of management intensity, landscape diversity measured with Management Index	Mixed (Trophic guild-dependent)	Williams-Guillén and Perfecto (2010)
Natural enemies of pests	Meta-analysis	Landscape complexity metric consider % natural habitat, % non-crop habitat, % crop, habitat diversity measured using Shannon and Simpson indices	Positive	Chaplin-Kramer et al. (2011)
Birds	Original	Coffee farms in sites of mixed cropland and habitat vs. separate areas of intensive agriculture and habitat	Positive	Railsback and Johnson (2014)
Parasitic wasps and flies	Original	Rotatory organic crop fields ranging from homogenous cover of annual crops to primarily forest trees and native shrubs within 500 m and 1500 m radius	Positive	Letourneau et al. (2015)
Bees and wasps	Original	Historical land cover change using spatial analysis within 1, 2, 5 and 10 km radii	Positive	Senapathi et al. (2015)
Birds and bats	Review	Cacao, coffee and mixed fruit orchards and tropical forest sites, comparison among forest, agroforestry and agricultural systems	Mixed (Taxa-dependent)	Maas et al. (2016)
Arthropods enemies of aphids	Meta-analysis	Proportion of cultivated land within a 1 km radius around each plot	Positive	Rusch et al. (2016)
Wild bees	Original	50 ha landscape plots in agricultural areas with increasing cover of semi-natural and natural vegetation patches	Positive	Bukovinszky et al. (2017)
Butterflies and farmland birds	Original	Proportion of arable field cover	Positive	Jonason et al. (2017)

Ceballos and Ehrlich (2002) made an indirect estimation of mammal population loss globally, by comparing present and historic ranges of 173 declining species, reaching a collective loss of 50% of range area. Regarding bird populations, Gaston et al. (2003) estimated a loss of approximately 22% of breeding bird individuals so that an average of 87 billion breeding bird individuals remain from approximately 112 billion estimated before 1700, which is considered the starting date for development of the current pattern of LUCC due to agriculture.

Global declines in pollinator populations are widely recognised (Biesmeijer et al. 2006, Gallai et al. 2009, Potts et al. 2010) and habitat loss is considered the main threat, particularly for habitat and plant specialists (Ricketts et al. 2008, Potts et al. 2010, Winfree et al. 2015). Equally, decline in predator and parasitoid populations due to habitat loss has been reported (Williams-Guillén and Perfecto 2010, Letourneau et al. 2015).

Population losses through microclimatic changes and edge effects

LUCC causes microclimatic changes in the remaining patches of ecosystem related to temperature, wind and humidity (Meyer and Turner 1992). There is evidence that deforestation can modify local rainfall and droughts pattern, changes in moisture and humidity can also negatively affect canopy, understorey and litter organisms and can increase fire frequency in tropical and arid ecosystems (Goldammer and Seibert 1990, Rao 2009), increasing the mortality of animal populations.

Along with climatic modification, physical changes diminish animal habitat suitability by reducing the quantity and quality of nesting, sheltering, and foraging sites (Frumhoff 1995). These changes can affect ecological interactions, survivorship, reproductive fitness and distribution of populations, particularly for highly specialised organisms (Dale 1994, Afrane et al. 2006, Rao 2009). Finally, the decrease in population sizes at the interface between two land cover types, known as the edge effect, is also enhanced by habitat fragmentation, caused by deforestation (Levin et al. 2009).

Population losses through pest proliferation and chemical pest control

Environmental changes caused by LUCC may adversely affect biological control processes. Spatial and temporal distribution and proliferation of insects, weeds and pathogens is largely determined by climate, therefore microclimatic changes in temperature, light and water supply can drive overpopulation of pests (Rosenzweig et al. 2001). Pest proliferation has detrimental consequences for ecosystems (Chapin et al. 2000, Wilby and Thomas 2002, Foley et al. 2005). For example, *Imperata cylindrica*, an aggressive indigenous grass, which colonises forest lands of Asia that are cleared for slash-and-burn agriculture, forms a monoculture grassland with no vascular plant diversity and few mammalian species in comparison with the native forest (Chapin et al. 2000).

Crop pests produce major losses for crop yields, therefore, farmers have resorted to the use of pesticides as a means of control. In the last six decades, there has been a dramatic increase in the use of pesticides. Along with agricultural intensification, herbicides, insecticides and fungicides have produced highly negative effects on species abundance and diversity (Geiger et al. 2010, Isenring 2010) and also threaten water quality (Vymazal and Březinová 2015) and human health directly (see Budzinski and Couderchet 2018) . There is evidence of the adverse effect of chemical pest control on farmland and wildlife populations worldwide (e.g. amphibians and reptiles, Gibbons et al. 2000, farmland birds, Boatman et al. 2004, benefitial arthropods, Desneux et al. 2007). Direct adverse effects include higher mortality due to poisoning, reduced fecundity and detrimental changes in physiology and behaviour. Indirect effects include reduction of habitat, due to destruction of non-invasive vegetation, reduction of food resources for predators by indiscriminate elimination of arthropod populations and imbalance in ecological interactions.

Impacts of biodiversity losses on provision of regulation faunal ecosystem services

It is sensible to assume that, by losing populations of providers, the production of ES might be compromised. However, it is crucial to understand the mechanisms that affect provision first. Several studies have evidenced the underlying reasons for the negative effect of population losses on FES production as outlined below.

Species richness loss

Regarding animal pollination, the high diversity in morphology and reproductive strategies of plants requires a similar diversity of pollinators (Blüthgen and Klein 2011). Therefore, a decrease in pollinator diversity potentially causes a decline in wild plant and crop diversity (Biesmeijer et al. 2006, Potts et al. 2010), as well as reduced crop productivity. Blanche and Cunningham (2005) observed a highly significant reduction in fruit set due to pollinator exclusion in atemoya crops. The risk is greater for wild or crop species that rely on a narrow range of pollinator species. Although the threshold of diversity, required to maintain pollination stability, depends on the biology and variety of crops, landscape structure and regional pollinator community, the evidence suggests that stability is higher with a diverse and abundant pollinator community (Klein et al. 2007).

Equally, a detrimental effect on natural pest control in crops has been identified due to a reduction in natural enemy diversity (e.g. rice crops, Drechsler and Settele 2001, Wilby and Thomas 2002, cacao plantations, Maas et al. 2013, coffee plantations, Karp and Daily 2014). Straub et al. (2008) indicated that higher diversity of

predators implies higher complementarity on functional roles: feeding on different pest species, at different life stages of the pest, using diverse strategies and differential partitioning of space and/or time (e.g. eating pest insects from different parts of the plant or during different seasons). This explanation could also be applied to parasitoid species.

Human disease control can be affected by reduction in species richness. A 'dilution effect' (*sensu* Keesing et al. 2006), where increased species diversity reduces disease risk for individual species, has been described for some diseases (e.g. tick-borne diseases, Norman et al. 1999, Ostfeld and LoGiudice 2003, viral pulmonary disease, Ruedas et al. 2004, mosquito-borne diseases, Ezenwa et al. 2006, Allan et al. 2009). This indicates richness loss can lead to more disease. Keesing et al. (2006) provides a detailed explanation of the mechanisms through which higher species richness decreases disease risk, including: reducing the rate of encounter between susceptible and infectious individuals, reducing the probability of transmission given an encounter, decreasing the density of susceptible individuals, increasing the recovery rate and increasing the death rate of infected individuals.

Seed dispersal is also affected by diversity loss. García and Martínez (2012) found a clear positive relationship between richness of frugivorous birds and all components of seed dispersal (i.e. seed richness and abundance and arrival and colonisation rates). Just like pollination and biological control, this suggests the existence of functional complementarity and/or facilitation amongst dispersers.

In general, even though initial species loss can be compensated by remaining species with similar functions, significant species loss will eventually reduce provisioning of FES. Therefore, to secure FES production, it is essential to conserve species richness.

Population loss

Along with species richness, population size or abundance, are determining factors for FES provision. Since population losses are higher than diversity losses (Ceballos and Ehrlich 2002, Gaston et al. 2003), these can have major implications on the magnitude and quality of FES provision.

Losses in pollinator populations produce a negative impact in wild plant communities, affecting the integrity of natural vegetation (Williams 2002, Biesmeijer et al. 2006). Additionally, population declines reduce crop production (Kremen et al. 2002, Larsen et al. 2005, Klein et al. 2007), causing important economic losses (Losey and Vaughan 2006, Gallai et al. 2009) and jeopardising food sufficiency worldwide (Aizen et al. 2009).

Equally affected is the pest control service, where abundance of natural enemies, predators and parasitoid species, largely determines the abundance of species that can become pests (Drechsler and Settele 2001, Mols and Visser 2007, Railsback and Johnson 2014). Like pollinators, losses in natural enemy populations cause losses in natural and agricultural systems (Losey and Vaughan 2006, Oerke 2006).

Regarding the disease control service, population size of hosts has a complex effect on transmission dynamics. Through model-based analysis, Norman et al. (1999), and

Gilbert et al. (2001) suggested that intermediate abundances of non-viraemic hosts (i.e. where pathogens do not enter the bloodstream) allow persistence in viraemic hosts, whereas high or low abundances lead to vector fadeout. Keesing et al. (2006) provided an example of how variation of population sizes of two rodent species through time affects disease spread: when there is a high density of chipmunks, there is a reduction in tick burdens on white-footed mice (the most competent reservoir for the Lyme bacterium). Losses in populations can lead to unpredictable effects on spread of vector transmitted diseases.

Decline in frugivorous populations reduce availability and quality of seed dispersal services (McConkey and Drake 2006, Peres and Palacios 2007). McConkey and Drake (2006) demonstrated that there is a threshold in population size for service provision; this is when the functionality of dispersers is lost, even before the individuals become rare. Therefore, the losses in disperser populations should not be dramatic to have a great impact on the seed dispersal service.

Thus, a decrease in abundance of FES providers has a negative impact on FES provision. Even though the reduction is small, the consequences on FES production can be significant given the complex interactions amongst the providers and the ecosystem functioning. Population losses imply more immediate effects than the loss of richness.

Potential impacts of future land use and cover change on faunal ecosystem service provision

While the understanding of the effects of current LUCC on ES provision has increased (Nelson et al. 2010), few studies have assessed the potential effects in the future (Nelson and Daily 2010). One of these is the assessment made by Lawler et al. (2014). They used LUCC models to assess the effects on the provision of carbon storage, timber production, food production and wildlife habitat. They projected LUCC from 2001 to 2051 for the United States under two scenarios: 1) a large increase in croplands (28.2 million ha) due to a high crop demand, mirroring conditions starting in 2007; and 2) a loss of cropland (11.2 million ha) mirroring conditions in the 1990s. These scenarios result in large differences in land-use trajectories that generate increases in ES from increased yields (even with declines in cropland area) and >10% decreases in wildlife habitat.

Mulligan (2015a) assessed the effects of agriculturalisation in Brazil and Colombia on carbon storage and sequestration, water services, hazard mitigation and species richness and endemism. He projected LUCC forward to 2100, using historic rates of conversion with new areas of agricultural growth based on agricultural suitability, proximity to current deforestation fronts and current and likely new transport routes, under two scenarios: 1) change is excluded from occurring in current protected areas and 2) change occurs both within and outside of protected areas. In both scenarios, there is a decrease in services, although it is lower in the first scenario. Similarly, Mulligan (2015b) assessed the effects of the same scenarios on these same services pantropically

from 2010 to 2050. Results suggest rapid agriculturalisation in the tropics implying considerable threats to the remaining natural capital and ES provision.

Regarding FES, Aizen et al. (2009) modelled the potential expansion of cropland and the resultant decline of pollinator populations. Based on annual data compiled for 45 years (1961–2006), they estimated a decrease of 8% in agricultural production due to loss of pollinator population. Crops with the least yield growth over the last five decades generally had the greatest expansion of cultivated area – including avocado, blueberry, cherry, plums and raspberry, which are highly pollinator-dependent. Therefore, they predict an increase in cultivated area, particularly in the developing world – mostly distributed in the tropics. Potential effects of future agriculturalisation on other FES remain to be evaluated.

Although there is still much to know about the future impacts of LUCC on FES provision, it seems possible to assess changes in supply in relation to agriculturalisation.

Expected demand for regulation faunal ecosystem services

ES demand is the sum of ecosystem goods and services currently consumed or used in a certain area over a given time of period (Burkhard et al. 2012). Therefore, to assess demand for ES – or FES – we need to know the factors determining their use in order to infer changes in demand as these factors change with agriculturalisation. For instance, the increasing demand for food, derived from population growth, the growing diversification of human diet, particularly in industrialised nations and globalisation in food trade have increased demand for many animal-pollinated crops. This is likely to continue in the future (Aizen et al. 2009).

World population is expected to reach 9 billion people by 2050 and would require raising overall food production by 70% (FAO 2009). Production in the developing countries would need to almost double. This implies significant increases in the production of several commodities, including crops (Alexandratos and Bruinsma 2012). Since agricultural land has a high demand for regulation ES and FES (Burkhard et al. 2012), such as pollination, natural pest control or nutrient regulation, an increase in demand for these services is expected.

Today, the developing world represents more than two thirds of global agricultural production and cultivated land and supports agriculture, which per unit of production, is 50% more pollinator-dependent than that of the developed world (Aizen et al. 2009). Along with the increase in food demand, the shortage in pollinator population might result in an increase in demand for agricultural land (Aizen et al. 2009), since per unit area crop yield may be reduced in the absence of pollinators (Morandin and Winston 2005, Aizen et al. 2009), causing, in turn, more extensive demand of FES provision.

Human induced changes might increase the demand for natural disease control. For instance, the development of irrigation systems is likely to increase the risk of contracting diseases such as dengue and malaria, by favouring the breeding of vectors,

like flies and mosquitoes, in areas where they were absent or rare (Fuller et al. 2012). Irrigated cropland has expanded considerably since 1970 and is projected to increase a further 20% worldwide by 2030, reaching almost 2,500,000 km^2 (Turral et al. 2010). Therefore, an increase in vector-disease outbreaks may be expected, as vectors may disperse to newly irrigated areas (Fuller et al. 2012).

Global forest area is projected to continue to decrease over the next years, although at a lower rate compared with the beginning of the century, declining from 0.13% to 0.06% per year by 2030 (d'Annunzio et al. 2015). This projection of forest area is the net result of increase in some regions and decrease in others. Faunal seed dispersal is a service that might help to regenerate and shape the forest structure in these areas, by allowing the seed movement of animal-dependent tree species. However, in general, based on the past and current information, the projections suggest an increase in FES demand due to agricultural expansion at the same times as there is a reduction in FES supply.

Conclusions

Ecosystem functions deliver final benefits or goods through the provision of ecosystem services where there is demand for them. To achieve proper management, conservation and valuation of such functions or of regulation ecosystem services and FES, an accurate characterisation is essential and understanding the providers of these services is a significant part. Animal populations are key providers of regulation services and simultaneously can be source of disservices. To secure the service provided and minimise disservices, it is imperative to continue studying their role, to understand the potential implications of their loss and to use this evidence base to advise conservation and sustainable land use.

We identified two components of faunal diversity as influential to FES provision, richness and abundance. Richness brings functional diversity and complementarity, improving the range of FES provision, while a higher number of species improves the magnitude and spatial distribution of provision, since it is abundance that determines the occurrence of these services. Speciose systems with low species abundance may have low or null FES provision.

Animal species may also be a source of disservices to people. We identified invasive and native species pest outbreaks as the most common sources of disservice. Animal populations can be the main actors or can act as vectors of viral, bacterial or fungal pests. The evidence suggests that invasive species can be an indirect source of disservice when disrupting the service provision by native species, while native species may impact directly as crop pests, human disease vectors or crop raiders.

Several studies suggest that agriculturalisation has negative effects on FES providers due to landscape homogenisation, habitat loss and fragmentation, microclimatic changes and population imbalance, causing species and population losses. This in-

creases the occurrence of disservices, impacting FES production through the decrease of functional complementarity — in the case of pollination, seed dispersal and pest control — or dilution effect — for human disease control and increasing crop and disease pest populations and wildlife-human conflict.

Few studies have addressed potential effects of LUCC on FES provision under different scenarios of agricultural change. LUCC models can be used to drive models for current and future FES provision. Such analyses are particularly important given the expected concomitant increase in demand for FES as land continues to be converted for agriculture.

The effects of land use change on FES providers have been assessed mostly at the local scale, using a range of approaches. To improve understanding of these effects at wider scales, it is desirable to develop a common approach to allow comparison and to identify land use configurations that maximise FES provision. For this, further research is required; first, to know the spatial distribution of FES providers; second, to identify the suitable conditions that allow FES providers to provide the FES and third, to relate these conditions to characteristics of land use and cover. Moreover, to date, the different FES have been evaluated independently: analysing them together can provide valuable information about distribution patterns, synergies and trade-offs amongst them.

Conservation prioritisation must factor in faunal ecosystem services (and disservices) as the most biodiversity-relevant of all ecosystem services and those which most closely links sites of conservation value that provide services with nearby sites of service use of agricultural and economic value. This will require the development of spatial models of faunal ecosystem services and disservices to compliment the ecosystem service models in existing tools such as Co$ting Nature (Mulligan et al. 2010, Mulligan 2015b) and InVEST (Tallis and Polasky 2009) and to drive these for baseline and scenarios of land use using LUCC models.

Maximum robustness of modelling results for policy formulation is achieved by using an ensemble of ecosystem service models, as has been common practice with climate models for decades. Each rigorous new approach to modelling faunal ecosystem services that is globally applicable and inter-operable or capable of comparison with existing models, can be a valuable contribution to improving our understanding of this important class of ecosystem services.

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